Development of cork-wings on certain trees. III.

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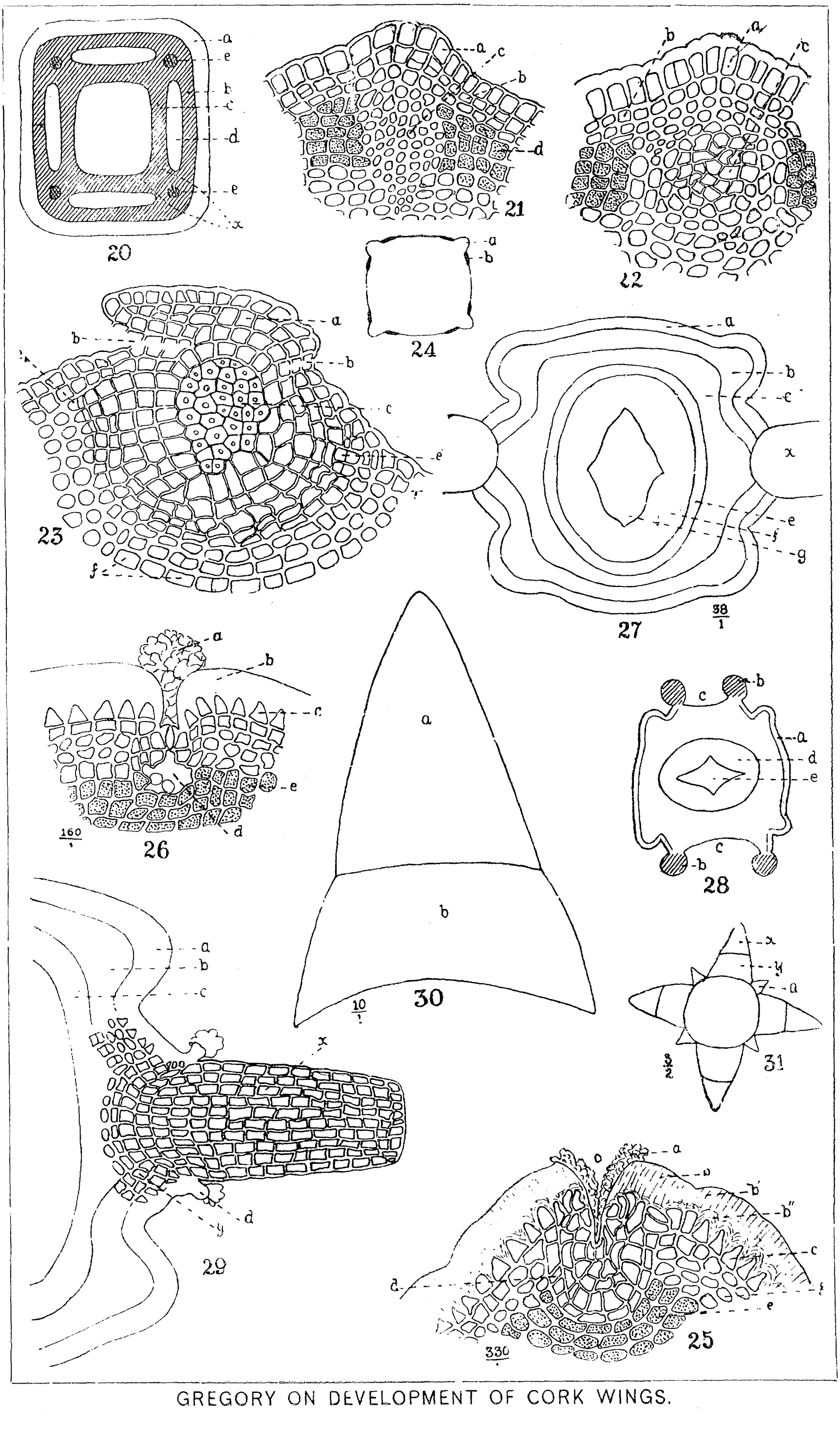
(WITH PLATE XXV.)

Of the genus Euonymus, the species now known as alatus, formerly described as *Celastrus alatus* Thunb., presents the most marked and striking example of what is known as cork-wings. The first important consideration on taking up the study of the wing in this genus is, that we have no longer to do with large trees, but with small ones and shrubs. One of our own native varieties, E. Americanus var. obovatus, Gray describes as trailing with rooting branches. Another species has small rootlets scattered over the branches. Closely connected with this fact is another of equal importance, that is, the lasting nature of the epidermis, or the length of time that some part of the surface of the stem performs the function of assimilation. Of the thirteen kinds of Euonymus examined, only five may be said to be winged in the sense in which we have used this term. Nearly all the others, however, present some features which are of use in determining the probable reason for this peculiar formation, exhibited in its strongest form in Euonymus alatus. A complete study of the periderm development of this genus would lead to a more extended treatment than was intended when limiting the study to the development of cork-wings. Certain parts of this subject must therefore be reserved for future consideration, and only those kinds described here which are really winged. These are E. alatus, E. Europæus and three varieties of the latter species, variegata, ovata and purpurea. A comparative study of these five kinds shows little difference existing in the anatomical structure of the wing of Euonymus Europæus and its three varieties. Any one of these may be described as illustrating a weak and less developed form of wing which finds its complete development in E. alatus. The structure of the primary rind of these four kinds is very nearly the same. The mechanical support, which in most dicotyledons and gymnosperms is furnished this rind by means of the bast fibers of the primary vascular bundles, is here wanting. In place of these are two cylinders of collenchymatic cells. These cylinders are connected at each corner by collenchymatic tissue extending from one to the other. This will be readily understood from the diagram, fig. 20. In this, *a* represents the epidermal layer; *b*, the



GREGORY ON DEVELOPMENT OF CORK WINGS.

outer cylinder of collenchymatic cells; *c*, the inner, and *d*, the thin-walled chlorophyll-holding cells, which serve the purpose of assimilation, and also to separate the collenchymatic tissue of the rind into the two cylinders. At each corner, *x x*, the collenchymatic tissue extends through to the young phloem tissue. In the species and in the varieties purpurea and variegata the corners are further strengthened by a cluster of extremely thick-walled bast fibers, and it is here at the corners that the wing formation begins. The time varies according to several conditions. One example of E. Europæus just brought in from the tree, September 28th, has one stem on which wings are forming on the second internode, while this is only one-half centimeter in length. On the same plant, another stem has fully 20 centimeters of its length without any appearance of wings. Several internodes of this are fully developed in length, and the lines of bast cells are visible along the four corners.

The wing development on a branch of the variety purpurea was studied from its beginning. A cross section at the distance of $\frac{1}{2}$ centimeter from the growing tip of stem shows the tissues of the rind in a formative stage. The outer wall of the epidermal cells is covered by a thin cuticle, the cells themselves are large, nearly isodiametric, and with thin walls; below the epidermis are two layers of thin-walled cells without chlorophyll, then 4 or 5 layers of parenchymatic chlorophyll-holding cells, and below these again several layers of colorless cells. At the corners of the stem (see fig. 21) the cells connecting the outer and inner cylinders of colorless cells are thick-walled and more or less collenchymatic in structure. A section cut at 3 centimeters from the tip of the stem shows that several important changes have occurred. The two cylinders of colorless cells now begin to take on a collenchymatic appearance, the walls having thickened considerably. The cells of the epidermis are in a state of rapid growth and division, new cells being added to the outer cylinder, whose walls rapidly thicken, as may be seen by sections at the distance of 5 and 7 centimeters from the tip. The cells in the center of the group in the corners (see *c*, figs. 21 and 22) are seen to have increased in diameter, while at the same time their walls are much thinner. These are the cells that afterward become the thick-walled bast fibers. (See *c*, of fig. 23.) There is just here a point of interest in regard to the origin of these bast fibers. Connected with it are also some other facts noted while making this study;

their consideration at the present time would lead us away from the subject in hand and it is therefore deferred. After the bast cells are well developed there begins a change in the character of the remaining collenchymatic cells lying immediately below them; these begin to stretch tangentially, then to grow and divide by radial walls, so that the circumference of the stem increases more rapidly at the four corners than elsewhere, and at this point, and apparently to meet this emergency, the phellogen layer of the cork-wing arises. A layer of collenchymatic cells extending entirely around the bast cells and joining those under the epidermis becomes the phellogen layer of the cork-cells. In using the word collenchymatic here, it must be understood as referring merely to the shape and thickness of the wall, and not to its nature as permanent tissue. The entire cells of the rind are up to this time in a growing, changing condition.

The origin of the cork-cells may be plainly seen on a section cut at a distance of 25 centimeters from the tip. Here at the points marked *e e*, on fig. 23, may be seen very distinctly the last wall formed in the phellogen cells. It is extremely thin, while the opposite wall of the same cell is very thick. In order to follow the course of growth, the sections were treated as recommended by Sanio, first placed in ammonia, then carefully washed and mounted in glycerine. The rapid growth of the phellogen pushes out the corner cells carrying the bast cells, a break of the epidermis occurs on either side, see *b b*, of fig. 23; this goes on till a wing of some size projects from each corner. The usual narrow plate cells mark the end of the season's growth. It is seldom, however, that the second season adds very much to the size of the wing. In the variety ovata, which lacks the bast fibers, the second season's growth of cork-cells appears to spread out from the outer phellogen cells of the first, so the circumference is increased with but very little outlay of material. (See fig. 24.)

Taking up now E. alatus, there are four sharp thin wings extending along the internodes, not at the corners, but as nearly as may be exactly between them. The bright green of the assimilating cells shows in strips between the wings, forming a peculiar contrast in color with the brown of the wings. The structure of the rind differs from that of the varieties already described. The stem is sharply four-angled, but the chlorophyll-holding cells extend entirely around it. They consist of several layers very similar in character

to the palisade cells of the leaf. There are no bast cells in the corners. The beginning of the wing takes place ordinarily after the internode has reached its length. The first indication of it externally is a little line of brown flecks at equal distances from the ridges at the corners. These may easily be mistaken for lenticels, but on examination they are found to be the first stages of the wing which originates directly from the stomata. These are distributed thickly and evenly over the surface, are sunken quite deep, as is usual on stems or leaves with a thick cuticle.

This line of brown spots extends along the entire internode, and a cross section through the middle of one of them gives the appearance as in fig. 25. One or two thin sections distant from this strikes across the end of the brown fleck and shows its stomatic origin (see fig. 26). In fig. 25, the cells marked *d* are the phellogen cells, and by contrasting different sections it is seen that these originate in the chlorophyll-holding cells under the air space, and at least three or four layers below those lining it. In this way the cells immediately about the air space are pushed out by the growing cork cells, are more or less broken, and form a debris around the openings of the stomata (see *a* in figs. 25 and 26). In fig. 26 this debris comes from the chlorophyll-holding cells of the central portion which have been shoved over to the end. This exudation is the peculiar mark of this species, for it is sufficient to form a ridge on either side through which the wing pushes its way, and when grown appears to rest in it as in a sort of socket. That this socket forms no part of the wing, is seen from the fact that if the latter be forcibly broken from the stem, the socket always remains, and can only be removed by cutting. (See fig. 28, *d.*) Continuing now the description from the stage seen in fig. 25, new cells are rapidly thrown off by the phellogen layer toward the circumference, and these appear between the ridges in a wedge shape at first, but the phellogen layer rapidly increases the number of its cells by dividing radially, so that the wedge grows rapidly broader at the base. The plate cells mark the end of the year's growth; the second season it is again resumed and continued during the entire summer, quite as much material being expended in this way as in the preceding summer, and from the same layer of cells. There is generally a difference in the color of the two parts of the wing, the second year's growth being lighter. The assimilation cells between the wings remain active until the third season,

at which time there often begins the formation of four new ones, which fill up the spaces between the old ones, and thus the whole surface of the stem becomes covered with a periderm, and the phellogen layer becomes continuous. In other cases the intervening spaces are not covered by means of a regular wing, but the cork formation seems to occur about the same time under all the stomata, so that after a time the whole surface is covered by an irregular periderm which grows up nearly even with the sharply projecting wedges of the wings.

Euonymus Americanus has a rind very similar in structure to that of alatus; it has, however, bast fibers in the corners, but they lie below the chlorophyll-holding cells. No wings have been discovered on this species, but it is rather a suggestive fact that on some young branches a line of cork growth often occurs running along the internode, neither in the middle between, nor exactly at, the corners of the stem, but close by these projecting corners. This growth never develops into more than a little brown ridge along under the green one of the corner. It is well known that Euonymus verrucosus has warty projections of cork, which are said to arise from lenticels, though at the time of their origin there is no appearance of periderm, unless the outer cylinder, which we have described as collenchymatic cells, be considered periderm.

Now, if the origin of the wing formation in the preceding five kinds of Euonymus has been correctly traced, it would seem that the usual statement made in reference to the periderm formation of Euonymus is not literally correct when applied to these five kinds. The periderm does not originate from the epidermal cells, if by periderm is meant the corky growth covering older stems, but from certain layers of cells at a greater or less distance below the epidermis. The cells which are cut off from the epidermal layer form an additional support to the outer collenchymatic cylinder, which at first is only two layers in thickness. By means of these additional cells from the epidermis the number is increased often to six or seven layers.

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EXPLANATION OF PLATES XXII AND XXV.—The first six figures represent diagrammatically the phases of growth of the wings of Quercus macrocarpa. The first four represent one year's growth, the fifth and sixth slightly different phases of a stem of three year's growth; *a a*, the break of the periderm tissue along the line of the five angles; *o o*, the

sections of original periderm tissue separated by these fissures; *x x*, the new tissue formed from the phellogen cells after the fissures occur; *y y*, the girdle of narrow plate cells whose walls are of the same chemical nature as those of sections *o o*. The lines between the points *b b*, in figs. 2 and 3, show the band of cork-cells; after the first year's growth the whole circumference is covered by these bands.

FIG. 7. Shows appearance of cross-section of a one-year-old stem in the region designated by *b b*, in fig. 2. The letters correspond to those of fig. 2, except there is in this figure *z*, the parenchymatic cells of the primary cortex or rind, and *m* shows a cell which has recently divided, making three cells.

FIG. 8. Cross-section of one-half of a wing in the stage represented in fig. 4. Lettered to correspond.

FIG. 9. Cross-section of top of wing as represented in fig. 6, stem three years old; sketched after treatment with reagents, therefore walls somewhat distorted.

FIG. 10. Cross section of a stem four years old, natural size. Lettered as the previous figures.

FIGS. 11 to 13 inclusive. Acer campestre. Fig. 11 shows outline of cross-section of first year's growth of stem; *x*, a wing already straightened out along the margin, the hairs at *h* showing that the epidermis is still preserved here. Letters correspond as far as possible to those of Quercus figures.

FIG. 12. Anatomical sketch of cross-section of wing as represented in fig. 11 by the wings x^0 x^0.

FIG. 13. Cross section of a two-year's old stem, natural size.

FIG. 14. Acer monspessulanum; diagrammatic sketch of a cross-section of a two-year-old stem. Letters correspond nearly: *f*, fissure; *x*, first year's wing; *x'*, second year's wing.

FIGS. 15 to 19 inclusive. Liquidambar styraciflua. Fig. 15. Anatomical sketch, in part diagrammatic, of beginning of wing: *a*, the fissure at the opening of lenticel; *b*, fissure made by the cells growing below.

FIG. 16. Cross-section of second year's growth, exact outline; cut June 24th. *a* and *b*, fissures as in fig. 15, *b*; *x*, first year's wing; *x'*, second year's wing; *y*, narrow plate cells of first year; *y'*, those of second year.

FIG. 17. Cross section of two years' old stem.

FIG. 18. Cross-section of four-years' stem.

FIG. 19. Cross-section of six-years' stem.

FIG. 20. Diagram of rind of E. Europæus and varieties. *a*, epidermis; *b*, outside collenchymatic cylinder; *c*, inside cylinder; *d*, chlorophyll holding cells; *e*, bast fibers in corners; *x*, the collenchymatic cells extending to phloem cells.

FIG. 21. Corner of E. Europæus var. purpurea; cross-section cut from stem ½ cm long. *a*, epidermis; *b*, colorless cells below; *c*, collenchymatic cells of corner; *d*, chlorophyll-holding cells.

FIG. 22. Same as 21, but cut at a distance of 3 cm. from tip of stem. Letters as in 21, except that the cells *c* can no longer be called collenchymatic.

FIG. 23. Same as 21, but cut at a distance of 25 cm. from tip of stem. *a*, section of cells burst away from the remaining part; *b b*, the breaks on each side; *c*, bast cells now fully developed; *e e*, phellogen cells, one side of which still show their collenchymatic origin; *f*, elongated collenchymatic cells.

FIG. 24. Diagram of stem of E. ovata wing of first year's growth; *b*, cork growth of second year.

FIG. 25. E. alatus, beginning of wing. *a*, debris formed by the remains of chlorophyll-holding cells of stoma which lined the air space; *b*, heavy cuticle of epidermis in two sections as seen by *b′* and *b″*; *c*, epidermis cell; *d*, cells of phellogen layer; *e*, chlorophyll-holding cells; *f*, collenchymatic cell; *o*, opening of stoma.

FIG. 26. Shows the origin of growth in fig. 25 more plainly: *a*, the debris thrown to the end; *b*, cuticle; *c*, epidermis; *d*, air space of stoma; *e*, chlorophyll-holding cells.

FIG. 27. Diagram of young stem of E. alatus, with only two wings started: *a*, epidermis and outer cylinder; *b*, palisade cells; *c*, inner cylinder; *e*, young cells of phloem and cambium layer; *f*, wood cells; *g*, pith; *x*, wing broken off.

FIG. 28. Sketch of cross section at early stage, showing how much is gained in circumference by the wing formation. Only two started and not far developed: *a*, epidermis; *b*, debris around the opening of the stoma; *c*, space with no epidermis where wing belongs; *d*, wood; *e*, pith.

FIG. 29. Same as 25, but represents the wing well started: *x*, wing; *y*, phellogen cells; *a*, epidermis and outer cylinder; *b*, palisade cells; *c*, inner cylinder; *d*, cuticle and debris.

FIG. 30. Sketch in outline of a two-year-old wing: *a*, the first; *b*, the second year's growth.

FIG. 31. Cross-section of two-year-old stem: *x*, first year's growth of wing; *y*, second year's; *a*, little wing of second year.

A tramp in the North Carolina mountains. II.

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One of the first plants to catch the eye of a stranger in the mountains is the Rhododendron. Before we reached Asheville we began to notice its dark glossy leaves and beautiful pink clusters, brightening the woods along the track, and as we got further west it became abundant. All through the mountains we found the common R. maximum, and we never tired of looking at it. In the lower vallies it was past its prime, but on the highlands and along the ridges it was in full bloom, and the great thickets of dark green, thickly starred with the rose-colored flowers, were worth going far to see.

In Cashier's valley they find the purple-flowered R. Catawbiense, but not a single flower could we find still hanging to its branch.

Another, and the most interesting and remarkable member of the genus, is the R. Vaseyi. This, too, grows in Cashier's valley, over toward Chimney Top. We saw it growing with most of its interesting neighbors in the exten-